Review of the Discovery and Identification of Onychophora in Australia

N. N. TAIT, R. J. STUTCHBURY and D. A. BRISCOE

TAIT, N. N., STUTCHBURY, R. J. & BRISCOE, D. A. Review of the discovery and identification of Onychophora in Australia. *Proc. Linn. Soc. N.S.W.* 112 (2), 1990: 153-171.

Over one hundred years have elapsed since the first discovery of onychophorans in Australia. During that time six species were described, amidst considerable debate and controversy. More recent detailed morphological analyses have added two further species. However, we have recently applied molecular taxonomic techniques to the endemic fauna and identified over fifty previously unknown biological species. This review records the history of discovery of onychophorans in Australia as a basis for further studies.

Noel N. Tait, David A. Briscoe, School of Biological Sciences, Macquarie University, North Ryde, Australia 2109, and Robyn J. Stutchbury, Geoscience Awareness Program, 1 Carisbrook Street, Lane Cove, Australia 2066; *manuscript received 20 June 1990, accepted for publication 26 September 1990.*

INTRODUCTION

Species delineation and reconstruction of phylogenetic relationships are particularly difficult in groups of organisms which are morphologically conservative and where the numbers of individual specimens available for examination are low. In these cases it is often impossible to determine whether subtle variations in morphological characters are the products of intraspecific variation, or evidence for the existence of more than one species. However, morphological conservatism does not necessarily reflect lack of diversity in other biological attributes such as polynucleotide sequences, protein structures and physiology. Over the last decade taxonomists have turned increasingly to the techniques of molecular genetics to provide independent data to resolve some of the more difficult problems.

Among the invertebrate phyla the Onychophora are considered to be an extremely conservative taxon, with limited morphological differentiation amongst members of the extant fauna. Moreover, comparisons of current forms with the scanty, but ancient, fossil record display striking similarities. Fewer than 100 species are recognized within the phylum world-wide, with eight species belonging to seven genera in Australia (Ruhberg, 1985; Ruhberg *et al.*, 1988). Recently, we have begun applying molecular taxonomic techniques to the Australian Onychophora and revealed an unsuspected extensive diversity of over fifty distinct species (Tait and Briscoe, 1990). These findings have led us to review the existing literature on endemic onychophorans and to present here a history of that knowledge as a base for subsequent taxonomic publications. This history includes not only some unusual onychophorans, but also some of the more colourful characters of Australian zoology.

ONYCHOPHORAN RELATIONSHIPS

Members of this phylum are commonly known as peripatus, after the first genus described (Guilding, 1826), or velvet worms, in reference to the texture of their integument. They have been allocated to two exclusive categories as 'missing links' and 'living fossils' (Hill, 1950; Ghiselin, 1984). Although they were first included with the molluscs (Guilding, 1826), their curious combination of annelid and arthropod characteristics were soon appreciated (Macleay, 1829; Gervais, 1837). However, their arthropod

features were subsequently ignored by many authors including Grube (1853) who created the order Onychophora to contain peripatus within the annelids. Their arthropod affinities were clearly established with a more detailed account of their internal anatomy and especially the discovery of their, albeit primitive, tracheal respiratory system (Moseley, 1874). Indeed, the Onychophora were seen to correspond with the Protracheata, a hypothetical ancestral group of the terrestrial arthropods, proposed earlier by Haeckel (1870, cited in Moseley, 1874).

The phylogenetic significance of the Onychophora has not diminished despite the recent controversy regarding the origins of, and relationships among, the various groups of extant arthropods. The monophyletic view is that the large number of synapomorphies displayed by all arthropods cannot be explained by convergent evolution (Clarke, 1979; Boudreaux, 1979; Mangum *et al.*, 1985; Wright and Luke, 1989), and the Onychophora are considered to be a sister group to the Euarthropoda within the phylum Arthropoda (Ax, 1984; Wright and Luke, 1989). In contrast, evidence from comparative functional morphology and embryology may be interpreted to indicate a polyphyletic origin of the arthropods and hence elevation of the Uniramia, Crustacea and Chelicerata to phylum rank (for review see Manton and Anderson, 1979). In this reassessment, the Onychophora represent a key position in the evolution of the essentially terrestrial uniramians. Sperm ultrastructural studies have also provided evidence for a phylogeny linking the clitellate annelids with the Onychophora and the other uniramians (Jamieson, 1986; 1987). Until this controversy is resolved, perhaps by the use of molecular taxonomic techniques (see Field *et al.*, 1988), most texts adopt the impartial view and designate the Onychophora as a discrete protostome phylum. The fossil record of onychophorans is sparse, and interpretation of its earlier members somewhat controversial. Fossils approaching present day onychophorans in general lobopodial body organization have been identified as *Xenusion anerswaldae* from the Early Cambrian Baltic (Pompeckj, 1927; Jaeger and Martinsson, 1967; Krumbiegel *et al.*, 1980); *Aysheaia pedunculata* from the Middle Cambrian Burgess Shale of British Columbia (Walcott, 1911; Whittington, 1978) and *A. prolata* from the Middle Cambrian Wheeler Formation of Utah (Robison, 1985). It has been suggested that these fossils be included as a taxon, Xenusia, of equal rank to the Onychophora and Tardigrada (Dzik and Krumbiegel, 1989).

Fossils with less contentious onychophoran affinities include *Helenodora inopinata* from the Late Carboniferous Mazon Creek beds of Illinois (Thompson and Jones, 1980) and in the rich assembly of the Late Carboniferous Montceau-les-Mines in central France (Heyler and Poplin, 1988). Both these fossil localities contain terrestrial and aquatic plants and animals, and so may represent the earliest record of terrestrial onychophorans. As yet, no fossil onychophorans have been identified from land masses where they presently exist.

The present day zoogeography of onychophorans is essentially one of Gondwanan origins, from tropical to Southern Hemisphere cool temperate regions (Brinck, 1956). They are divided into two families, the Peripatidae (Evans, 1901a) from tropical regions of West Africa, South-east Asia and central and South America and the Peripatopsidae (Bouvier, 1907) from South Africa, Australasia and Chile. Since both families are represented in Africa and South America, it would appear that the two families diverged before the break-up of Gondwana some 130 million years ago (Ghiselin, 1985).

Body organization and way of life are essentially similar in the one hundred or so extant species. Their inability to control water loss (Manton and Heatley, 1937; Manton and Ramsay, 1937; Morrison, 1946; Dodds and Ewer, 1952) confines them to terrestrial microhabitats of high humidity in rotting logs, under logs and stones, leaf litter and soil. They are negatively phototaxic (Holliday, 1942; Manton, 1938a; Brinck, 1956), forage

at night (Read and Hughes, 1987) and, in the laboratory, maintain a nocturnal activity rhythm (Alexander, 1957; Newlands and Ruhberg, 1978). They are active predators enmeshing their prey in jets of sticky slime ejected from a pair of modified limbs, the oral papillae, located on either side of the head. The prey is then torn open by the mandibles and immobilization completed by injection of saliva, which may also partially digest the flesh prior to it being sucked back into the mouth (Read and Hughes, 1987).

However, in their reproductive biology the Onychophora display great diversity. Female reproductive strategies span the spectrum from oviparity with yolky shelled eggs (Dendy, 1902); to ovoviviparity with yolky eggs (Sheldon, 1888; Evans, 1901b; Anderson, 1966); to viviparity with yolk-free eggs (Manton, 1949) and placental viviparity (Anderson and Manton, 1972).

Males generally produce spermatophores (Storch and Ruhberg, 1977). In species of *Peripatopsis* spermatophores may be deposited on any part of the body of the female (Sedgwick, 1885; Manton, 1938a; Ruhberg, 1985). Invading haemocytes bring about the destruction of the cuticle and the spermatophore envelope at their point of contact and the spermatozoa travel through the haemocoel to the ovary which they penetrate to reach the lumen (Manton 1938b). In contrast, spermatophores of the genus *Peripatus* are reported to be implanted directly into the female genital opening (Lavallard and Campiglia, 1975; Schaller, 1979). In the genus *Paraperipatus*, males lack the ability to produce spermatophores (Willey, 1898; Cuénot, 1949) and insemination is presumably direct (Schaller, 1979).

The recent discovery of a number of previously undescribed Australian onychophorans, with male head structures involved in sperm transfer, indicates that male reproductive biology may be as diverse as that of their female counterparts (Tait and Briscoe, 1989; 1990).

Historical Review and Discussion

Early Records

The first scientific record of an Australian onychophoran was made by Rudolf Leuckart, then Associate Professor of Zoology at the University of Giessen. In his report of the scientific achievements in the natural history of lower animals for 1860, he recorded that he could add to the list of known species of *Peripatus*, a new one from Australia, which (incorrectly) was distinguished by possessing sixteen pairs of legs (Leuckart, 1862).

The specimen was subsequently passed on to Mr H. Saenger, who included a short description of it, as *Peripatus Leuckartii* (Saenger, 1869). Subsequent changes in spelling and synonomies are given in Table 1. Saenger's account gave a marginally more precise locality 'north-west of Sydney' and established the correct number of walking legs (15 pairs), but the reported lack of claws on the first pair was later to provide confusion. Saenger's paper (1869) was reviewed by Leuckart in his reports for the years 1868-69 and 1870-71 (Leuckart, 1869; 1871).

Almost twenty years elapsed after Leuckart's (1862) note before Australian peripatus were again mentioned in the scientific literature. In 1886 two specimens from Cardwell in North Queensland were sent to Mr Henry Tryon of the Queensland Museum (Tryon, 1887), subsequently exhibited in Sydney in November 1886, and then lost. Tryon next met with peripatus under dead wood in a gully in Victoria Park, Brisbane, and, accompanied by Mr Frederick Skuse, under stones close to the Brisbane General Hospital. These specimens were exhibited to the Royal Society of Queensland on 15 April, 1887 (Tryon, 1887). This rediscovery of peripatus in Australia created such

interest that it was reported the next day in the 'Brisbane Courier' of Saturday, 16th April, 1887, where a half column was devoted to a very scientific discussion of its biology and significance.

In the same year, Professor Jeffrey Bell, of King's College, London, and the British Museum of Natural History, published a notification of two specimens sent to him by Dr. Edward Ramsay, Curator of the Australian Museum, Sydney, and collected in the 'Queensland Scrubs' near Wide Bay (Bell, 1887). The specimens were forwarded to Adam Sedgwick, of the University of Cambridge, and an account of them was incorporated into his monograph on the genus *Peripatus* (Sedgwick, 1888). Skuse (1897) later claimed that the specimens referred to by Sedgwick as coming from Wide Bay were in fact collected, by him, under stones close to the Brisbane General Hospital and Acclimatisation Society's Grounds on 3rd April, 1887, presumably on his outing with Tryon.

1887 also marked the first in a series of papers on peripatus by Mr. Joseph James Fletcher, the newly appointed director and librarian of the Linnean Society of New South Wales. This was a note and exhibition of a specimen with 15 pairs of claw-bearing legs obtained from Warragul in Victoria (Fletcher, 1887). No comparison was made with the Queensland specimens but Fletcher considered it of sufficient interest as a record of the wide distribution of peripatus in eastern Australia. Following the discovery of peripatus in Queensland and Victoria, an accurate locality in New South Wales was provided by the exhibition of a specimen from Cassilis (Olliff, 1887).

In the Australasian section of his 1888 monograph, Sedgwick included a description of *P. novae-zealandiae* (Hutton 1876) and *P. leuckartii* which he based on the two specimens from Wide Bay (or, according to Skuse (1897), from Brisbane) Queensland. The diagnosis of *P. leuckartii* was: Australian peripatus with fifteen pairs of legs, an accessory tooth on the outer blade of the jaw (absent in *P. novae-zealandiae*) and a white papilla on the ventral side of each of the last pair of legs in the male (absent in *P. novae-zealandiae*). Sedgwick also noted that the genital pore of the female *P. leuckartii* — was situated on the tip of a conspicuous protuberance. This feature, an ovipositor, was later to assume importance in indicating an oviparous mode of reproduction.

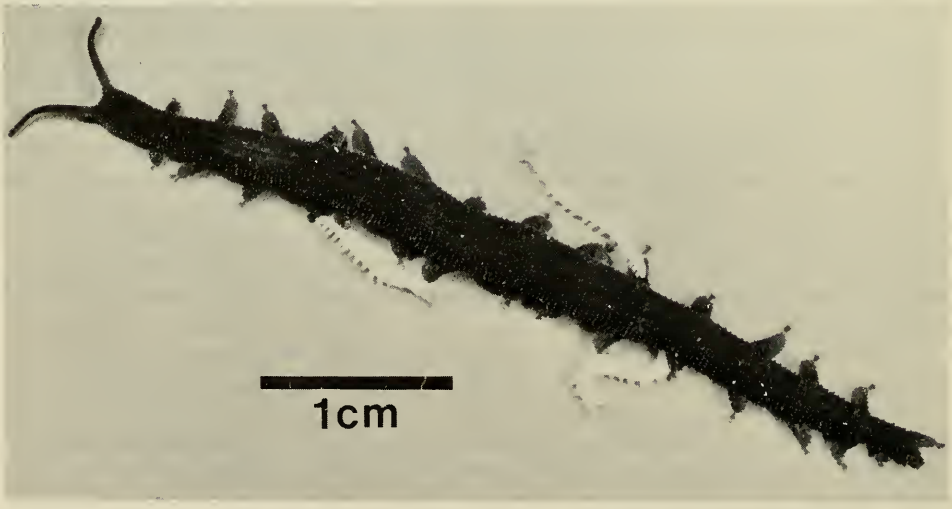

Fig. 1. Female and new born young of the ovoviviparous *Euperipatoides leuckartii*, the first species of an onychophoran described from Australia.

Fletcher's enthusiasm for onychophorans apparently increased during 1888, as evidenced by his presentation of three exhibitions. The first, on 27th June, noted that specimens collected near Wollongong were of a prevailing dull black or brown and red colouration, in contrast to the indigo-blue of those from Queensland, and foot-noted that dissection of one individual showed it to be pregnant (Fletcher, 1888a). Later, on 31st October, he exhibited the four newly-born progeny of one of his June specimens and noted their size (7mm when extended) and colouration (almost colourless to conspicuous pigmentation within a few days) (Fletcher, 1888b); see Fig. 1. On November 2nd, he exhibited, and noted the colour variation between, two specimens from Burrawang, near Moss Vale in New South Wales (Fletcher, 1888c).

The known range of peripatus in New South Wales was extended over the next few years with Fletcher's receipt of specimens from Dunoon (on the Richmond River in the north), the Blue Mountains and, most surprisingly, from the Mount Kosciusko region (southern alps) (Fletcher, 1890). The last were collected by Mr. R. Helms in March 1889 at Pretty Point and Wilson's Valley at altitudes of over 1500 metres where, for some months of the year, the ground is frequently covered with over a metre of snow (Helms, 1890). Fletcher (1890) described the variation in colour of the specimens from each of the three localities. The prevalent colours were indigo-blue and red, either of which could predominate, with longitudinal stripes of light and dark colour most conspicuous in specimens with a maximum of red.

Before the turn of the century, predominantly dry inland onychophoran localities at Tamworth (Paulden, 1898) and Morec in the north-western plains (Waite, 1895), were added to Olliff's (1887) Cassilis record.

Meanwhile Arthur Dendy, of the University of Melbourne, had described two specimens collected at Warburton in Victoria (Dendy, 1889a; b); Dendy often published the same article simultaneously in a local and an overseas journal. Although possessing fifteen pairs of claw-bearing legs, they were so strikingly different from both *P. leuckartii* and *P. novae-zealandiae* in colour and pattern that Dendy considered that they belonged to a separate species.

Sedgwick lost no time in refuting Dendy's assumption that a new species designation was warranted (Sedgwick, 1889). He pointed out that specimens he had examined from both New South Wales (donated by Mr Olliff) and Queensland were identical and, therefore, he doubted the distinctiveness of any Victorian forms. Furthermore, the considerable colour variation exhibited within both *P. capensis* (Grube 1866) and *P. novae-zealandiae* indicated the danger of using colour in species identification. In a personal letter Fletcher also cautioned Dendy regarding the use of colour in species identification (Dendy, 1889c).

These communications seem to have had the desired effect. In his next article, Dendy described the colour variation in eleven specimens of peripatus collected near Ballarat, Victoria (Dendy, 1889c). The external features used in the diagnosis of *P. leuckartii* by Sedgwick were shared with the Victorian specimens. Thus Dendy was persuaded to accept only one species of peripatus so far described from Australia. In the handbook provided for the use of members of the Australasian Association for the Advancement of Science (AAAS) held in Melbourne in 1890, Dendy noted the significance of peripatus and the occurrence of *P. leuckartii* in Victoria (Dendy, 1890a).

A turning point came in 1890 with the description of a new species, *P. insignis*, from Macedon, Victoria (Dendy, 1890 b,c). This form was distinguished from *P. leuckartii* in possessing only 14 pairs of legs, and the absence of the accessory tooth on the outer blades of the jaw and the white papillae on the bases of the last pair of legs of males. The

female genital aperture was located at the tip of a prominent white protuberance (later termed an ovipositor).

The known distribution of peripatus was extended to include Tasmania in a note on the existence of a bleached specimen, possessing fifteen pairs of legs, in the Macleay Museum at the University of Sydney (Fletcher, 1890). Except for the locality being Tasmania, no other information accompanied the specimen, which no longer exists in the museum (Horning, 1989, pers. comm.). This is regrettable as the specimen raises an intriguing historical possibility. In his letter of 1829, William Sharp Macleay (Macleay, 1829) comments that there is a specimen of peripatus in the collection of his father, Alexander Macleay. If this specimen corresponded to the one viewed by Fletcher, it would represent the first Australian onychophoran, predating Leuckart by nearly 40 years.

In 1895 Professor Baldwin Spencer, of the University of Melbourne, collected specimens which he identified as *P. insignis*, at Dee Bridge, Tasmania (Spencer, 1895). He did, however, note the relatively large size of these individuals, in comparison to Victorian forms of *P. insignis*. This distinction later led Cockerell (1913) to name the Tasmanian peripatus after Spencer (Table 1). Flynn (1918) added further localities at Great Lake and near Hobart.

The year 1895 was also notable for the first collection from Western Australia. Five specimens from Bridgetown had fifteen pairs of legs but lacked an accessory tooth on the outer blades of the jaws (Fletcher, 1895). Were these animals a variety of *P. insignis* with an additional pair of legs, or *P. leuckartii* without an accessory tooth? They were to play an important part in an acrimonious dispute on the taxonomy and reproductive biology of peripatus which had developed between Fletcher and Dendy.

Viviparity, Oviparity and Taxonomy

Apart from Fletcher's observation of the sudden appearance in vivaria of juveniles (Fletcher, 1888b), nothing was known of the reproductive biology of the Australian species. Fletcher assumed that the young were born alive as viviparity had been described in various species of peripatus from other continents.

In May, 1891, Dendy obtained several specimens, with fifteen pairs of legs, and hence referable to *P. leuckartii*, from Macedon, Victoria, the type locality of *P. insignis*. One male and three females were maintained in a vivarium for long-term observation and on 31st July, several eggs were found deposited beneath and in the crevices of bits of rotten wood (Dendy, 1891a,b,c,d). The identity of the eggs was in no doubt as dissection of the genital tract of females revealed eggs of comparable form; very large, oval, and each enclosed in a very tough, thick membrane. In the eggs from dissected females this membrane appeared smooth, while in the deposited eggs it was exquisitely sculptured (Fig. 2). On the basis of these observations, Dendy concluded that *P. leuckartii*, as he had been persuaded to call the Victorian specimens with fifteen pairs of legs, was oviparous, that Fletcher's intimated conclusions regarding viviparity were in error, and that Fletcher had failed to notice laid eggs in his vivarium. Dendy expected the eggs to hatch in October, based on Fletcher's finding of juveniles in that month.

The response to this report of oviparity in Australian peripatus was immediate and critical. Sedgewick (1891) suggested that it was no more than a case of abnormal extrusion of undeveloped embryos induced by stress. This criticism entirely misrepresented Dendy's description of eggs with a thick shell, a development that does not occur in viviparous species.

Fletcher's criticism was even more overt (Fletcher, 1891a), stating that no matter what mode of reproduction occurred in peripatus from Victoria, those from New South Wales were definitely viviparous. He exhibited a series of twenty eight embryos

including individuals whose development was so nearly complete that they must have been close to parturition. He followed this by an exhibition of about one hundred specimens from the Blue Mountains, together with their progeny, prematurely-born young of an accidentally injured female, advanced embryos extruded during the drowning of their mothers, and dissected females showing the oviducts crammed with embryos (Fletcher, 1892a).

Fletcher elaborated a defense of his own conclusions and an attack on Dendy in a paper read to the Linnean Society of New South Wales on 27th April 1892 (Fletcher, 1892b). He appeared to be particularly incensed to read the claim (Dendy, 1891a,b,c,d) that '. . . hitherto little has been known of its habits and nothing of its mode of reproduction.' He tartly replied that he would have no difficulty in proving, even to Dendy's satisfaction, that the New South Wales peripatus was '. . . viviparous in 1888, that it is still viviparous in 1892, and that in the interval it was also viviparous . . .'! He pointed out that the first dissected specimen of *P. leuckartii* (Fletcher, 1888a) was full of advanced embryos similar to those found in South African *P. capensis* by Moseley (1874), and therefore in accordance with what was known of other species.

Fletcher was by no means convinced that Dendy's Victorian forms were oviparous, adding to the doubt already seeded by Sedgwick (1891). He stated that Dendy should have confined himself to Victorian peripatus and not generalized to include New South Wales forms. Nonetheless, he conceded, 'If the Victorian peripatus really is oviparous, then it is oviparous . . . also the mode of (its reproduction) will almost certainly differ from that of the New South Wales peripatus . . .'

Dendy replied to this criticism at the Hobart meeting of the AAAS (Dendy, 1892a) and provided further information to support his views (Dendy 1892b,c). First, he pointed out that it was Fletcher and Sedgwick who persuaded him that Victorian specimens should be referred to *P. leuckartii*. Second, Dendy was not aware of contradicting any statement regarding the mode of reproduction in the New South Wales form, for the simple reason that he could not find any definite statement for him to contradict. Dendy now fully admitted that he had been incorrect in his interpretation of the mode of reproduction in the New South Wales specimens but that he was, nevertheless, justified in his conclusions.

The solution to the whole difficulty was simple. Dendy's original opinion was correct and the Victorian form with fifteen pairs of legs was specifically distinct from *P. leuckartii*. He refrained, at the time, from giving it a name.

Meanwhile the catalysts of this acrimony, the eggs found on 31st July 1891 in Dendy's vivarium, had not hatched. One, dissected in October, surprisingly revealed no sign of an embryo but, by November, coiled embryos were evident within several eggs. Dissection of one of these revealed an advanced embryo. By April 1892 only three eggs remained. Nearly a year later, on January 3rd 1893, the one remaining egg was found to have split on one side and a young peripatus had emerged. Ironically, after seventeen months of patient vigilance, Dendy found it dead in the container (Dendy, 1893a,b). Although the eggs were maintained under artificial conditions, these observations indicated an extraordinarily long incubation period for this species and vindicated Dendy's proposition that Victorian peripatus were egg-layers. It would seem that the controversy should now have abated. This was not to be.

By this stage two named species were acknowledged in Australia, *P. leuckartii* and *P. insignis*, together with the unnamed Victorian oviparous form studied by Dendy. Even this meagre consensus was disturbed by Dendy in his presidential address to the biological section of the AAAS meeting in Brisbane in January, 1895. Dendy reported a recently acquired translation of Saenger's (1869) diagnosis of *P. leuckartii*, obtained from Professor Baldwin Spencer (Dendy 1895a). He suggested that the description more

closely fitted *P. insignis*. i.e. fourteen pairs of claw-bearing legs and the first, clawless legs were really the oral papillae.

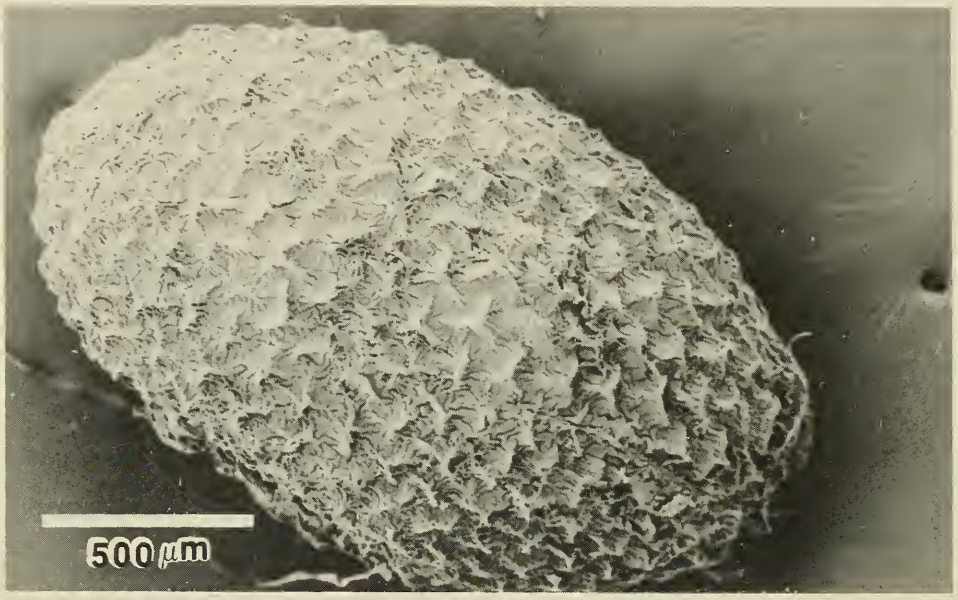

Fig. 2. Scanning electron micrograph of the sculptured egg of the oviparous *Ooperipatellus insignis*.

On his way to the meeting, Dendy had met with Fletcher in Sydney and discussed nomenclature (Dendy, 1902). They decided to each present a paper at the next meeting of the Linnean Society of New South Wales, Fletcher to confine himself to the viviparous form from New South Wales, and Dendy to the oviparous Victorian species. They agreed the latter should now be named. This arrangement did not last long. Fletcher received the specimens from Bridgetown, Western Australia which possessed fifteen pairs of legs (like *P. leuckartii*) but with the outer jaw blade morphology of *P. insignis*. The concept of erecting yet another species was too much for Fletcher, '. . . Australia would, I think, be oversupplied with as many as four species' (Fletcher, 1895).

Fletcher commented on variation in the form of the accessory tooth in the New South Wales specimens and that it would seem the number of legs was also variable (fourteen or fifteen pairs) especially as a New Zealand form with sixteen pairs of legs had recently been discovered and designated a subspecies *P. novae-zealandiae* (*suteri*) (Dendy, 1894a,b).

Thus Fletcher writes, 'The most satisfactory arrangement, in my opinion, would be to consider all the known Australian specimens of peripatus as referable to one comprehensive species with four varieties'. His species diagnosis is all encompassing, 'With fourteen or with fifteen pairs of claw-bearing, ambulatory legs; outer jaw blades without or with an accessory tooth, occasionally more, at the base of the main tooth; males smaller than females, with a pair of (accessory gland) pores close together and situated between the genital papilla and the anus; with a white or sometimes bluish tubercle, on which opens the crural gland, on each leg of the first pair only, or of the last pair only, or of all or only some of the pairs with the exception of the first, or of the first five.' The distribution was described as suitable situations in the tableland and coastal regions of

Queensland and New South Wales, Victoria, Tasmania, and Western Australia. The four varieties included:

i. *P. leuckarti* Saenger var. *typica* = *P. insignis*, Dendy. With fourteen pairs of claw-bearing legs; outer jaw blades without an accessory tooth. New South Wales, Victoria and Tasmania.

ii. *P. leuckarti* Saenger var. *occidentalis, var. nov.* With fifteen pairs of walking legs; outer jaw blades without an accessory tooth. Bridgetown inland from Perth, Western Australia.

iii. *P. leuckarti* Saenger var. *orientalis, var. nov.* With fifteen pairs of walking legs; outer jaw blades with one or several accessory teeth. Queensland and New South Wales.

iv. The Victorian *Peripatus* to be dealt with by Dr. Dendy. Victoria and Tasmania (probably for the bleached specimen in the Macleay Museum).

Thus Fletcher had taken up Dendy's tentative suggestion that *P. insignis* was the real '*leuckartii*' without reference to the type specimen.

From Fletcher's descriptions of the various subspecies of *P. leuckartii*, some indication of morphological differentiation is evident in the distribution of the crural glands in males. The extraordinary range outlined in the species diagnosis does not occur in each of the subspecies. Thus *P. leuckarti typica* has crural glands on all legs except the first five pairs, while in *P. leuckarti occidentalis* they are present on all legs except the first pair. *Peripatus leuckarti orientalis* is unusual in that while most individuals have a similar distribution of crural glands to *P. leuckarti occidentalis* some have a distinctive pattern with crural glands on the first pair of legs only. The first record of an individual with this .pattern was for a specimen collected in the Blue Mountains (Fletcher, 1891b). Subsequently as many as thirty individuals had been identified displaying this distribution of crural glands. It is evident that Fletcher's view of how many species of peripatus Australia could support prevented him from diagnosing specific differences and indeed in one subspecies, *P. leuckarti orientalis*, he could in fact have incorporated two species each displaying a distinctive pattern of crural glands in the males. The distribution of crural glands was later to receive prominence in the identification of Australian onychophorans (Ruhberg, 1985; Ruhberg *et al.*, 1988).

Apart from a short note on the extension of the distribution of a New Zealand species (Fletcher, 1900), this was to be Fletcher's last word on the subject of peripatus taxonomy.

Dendy's paper, confined as agreed to the Victorian egg-laying species with fifteen pairs of legs, was published next to Fletcher's (Dendy, 1895b) and in an abridged form (Dendy, 1895c). Dendy was presumably unaware of what Fletcher had done to the taxonomy of Australian peripatus and he provided a detailed description of the reproductive anatomy of *P. oviparus n. sp.* with an account of the formation of the egg membranes. This was the first report to correlate the presence of a large extensible ovipositor between the last pair of legs in females with the oviparous mode of reproduction. No comment was made about the possibility of *P. insignis* being oviparous although this species had been described as possessing a conspicuous ovipositor (Dendy, 1890 b,c).

The distribution of oviparous species was soon extended to include New South Wales and Queensland. Already Sedgwick (1888), in his description of *P. leuckartii* from southern Queensland, had noted the presence of an ovipositor, but this was not taken at the time as an indication of oviparity. Thomas Steel, an industrial chemist with the Colonial Sugar Refining Company in Sydney and twice President of the Linnean Society of New South Wales, made the next contribution. He had reported extensively on the colour variations, behaviour and sexual biology of viviparous specimens from the Moss Vale District, New South Wales (Steel, 1896). In the following year (Steel, 1897),

he noted the possible occurrence of *P. oviparus* between Exeter and Bundanoon, in the same general area as Moss Vale, based on a specimen with striking colour and a fully extended ovipositor. Furthermore, Steel re-examined the specimens collected by Helms at Mount Kosciusko (Fletcher, 1890) and noted that they too had conspicuous ovipositors and were, in all probability, *P. oviparus*. Spencer (1892) collected nine peripatus near Cooran in southern Queensland. Subsequent examination of one female revealed an ovipositor (Dendy, 1902).

The range of oviparous onychophorans, unknown elsewhere in the world, soon included New Zealand. In 1900 Dendy reported a species, from the South Island, which had fourteen pairs of legs and a conspicuous ovipositor in females (Dendy, 1900a,b). He proposed the name *P. viridimaculatus*. During the same year Fletcher (1900) exhibited specimens from the North Island which he referred to as *P. viridimaculatus*.

The first attempt at generic re-evaluation of the rapidly accumulating species of *Peripatus* world-wide, was by Pocock (1894). He proposed three genera: *Peripatus* to be retained for neotropical species; *Peripatopsis* for South African species; and *Peripatoides* for those from Australia and New Zealand. This led to the erection of many new genera within each of these geographical areas.

By 1900 Dendy had amassed enough information to propose that the three species of oviparous peripatus should be given a separate generic designation (Dendy, 1900c). The genus *Ooperipatus* was proposed to include:

i. *O. oviparus*, with 15 pairs of legs and an accessory tooth on the outer blade of the jaw. Victoria, N.S.W. and Queensland.

ii. *O. insignis*, with 14 pairs of legs and no accessory tooth on the outer blade of the jaw. Victoria and Tasmania.

iii. *O. viridimaculatus*, with 14 pairs of legs, no accessory tooth on the outer blade of the jaw and distinctive colour pattern. North and South Islands of New Zealand.

While each of these species was characterized by the presence of a conspicuous ovipositor, shelled eggs had only been identified in *P. oviparus* and *P. viridimaculatus*. Specimens of *P. insignis*, so far collected, were small and contained neither eggs nor embryos.

Thus by the turn of the century, six species of peripatus had been described from Australia and New Zealand, three of which were distinguished by the egg-laying mode of reproduction. Although Sedgwick cautioned against the erection of new genera (Sedgwick, 1908), the *ad hoc* erection of genera continued and *Peripatoides* became entrenched to accommodate the viviparous species; *P. leuckartii* in the east and *P. occidentalis* (elevated to species rank by Bouvier (1907)) and the later identified *P. gilesii*, in the west with *P. novae-zealandiae* and *P. suteri* from New Zealand. The genus *Ooperipatus* was also retained to include the oviparous species; *O. oviparus* from Victoria, New South Wales and Queensland, *O. insignis* from Victoria and Tasmania and *O. viridimaculatus* from New Zealand (Dendy, 1900c).

Having been the prime instigator of the recognition of oviparity in some species of Onychophora, Dendy culminated his contribution with a detailed description of the three egg-laying species from Australia and New Zealand (Dendy, 1902). Although Dendy was responsible for initiating the idea that the Victorian species with fourteen pairs of legs (*O. insignis*) was possibly the real '*leuckartii*' (Dendy, 1895a), he had abandoned this notion in his revision of the generic designation of the oviparous species (Dendy, 1900c). Dendy's observations of Leuckart's specimen at the Leipzig Zoological Museum finally confirmed that it was identical to the ordinary viviparous form with fifteen pairs of legs found in New South Wales (Dendy, 1906). Hence it was left to Fletcher to perpetuate the notion, that the real '*leuckartii*' had fourteen pairs of legs, in his

view of the taxonomy of Australian peripatus as one comprehensive species with *O. insignis* designated *P. leuckarti typica* (Fletcher, 1895). Steel concluded his contribution with an account of peripatus in the first edition of the Australian Encyclopaedia (Steel, 1925).

Later Discoveries and Revisions

In 1905 the Hamburg expedition to Western Australia, led by Professor W. Michaelson and Dr. R. Hartmeyer, collected onychophoran specimens at Lion Mill in the Darling Ranges, inland from Perth. These were distinctive in possessing sixteen pairs of legs, but shared with *P. occidentalis* the absence of accessory teeth on the outer jaw blade. Bouvier (1909a,b) named these *Peripatoides Woodwardi*. Prior to the German expedition, Mr. H. M. Giles, of the Zoological Gardens in Perth, had made several collections (Woodward, 1906) and sent four animals, from Armadale, southeast of Perth, to Baldwin Spencer who described them as *P. gilesii* (Spencer, 1909). Professor William Dakin, of the University of Western Australia, while attempting to identify onychophorans from Mundaring Weir in the Darling Ranges, recognised the potential synonomy of *P. gilesii* and *P. woodwardi* from such close localities. Comparisons of his specimens with type specimens of Spencer and the descriptions of Bouvier (1909a,b) confirmed the synonomy. The name *P. gilesii* took precedence by less than nine months (Dakin, 1914a,b).

Furthermore, comparison of *P. occidentalis* with *P. gilesii* resulted in a surprising conclusion (Dakin, 1920). Apart from the number of legs, the two species agreed in all other respects. This included the distribution of the crural glands as occurring on all pairs of legs. Dakin settled the conflicting reports of the number of pairs of these structures in the Western Australian species (Fletcher, 1895; Bouvier, 1900; Haddon, 1913) by pointing out the difficulty in identifying crural papillae from external examination due to variation in their state of protrusion. Careful dissection is the only way to reveal the correct number of papillae and their associated glands. On this basis Dakin concluded that the two forms were varieties of one species. Since *P. occidentalis* had precedence over *P. gilesii*, the former was retained. Thus Dakin reduced the number of species of peripatus in Western Australia from three to one.

The contribution made by the eminent zoologist, Bouvier, to the biology of Onychophora extends far beyond his naming of Australian species. His work, and a synthesis of others, is embodied in two large monographs (Bouvier, 1905a, 1907). Bouvier divided the Onychophora into two families: the Peripatidae (Evans, 1901a) to include the tropical forms from Africa, South-east Asia and central and South America, and the Peripatopsidae (Bouvier, 1907) from South Africa, Australasia and Chile. In his first publication on Australasian onychophorans he commented on the paucity of specimens from the region, held in the British Museum, but, nonetheless, noted that the male of *P. leuckarti orientalis* possessed crural papillae on legs two to fifteen inclusive (Bouvier, 1900). The species designation was later changed to *Peripatus orientalis* (Bouvier, 1902) and then to *Peripatoides orientalis* in a more detailed account of its anatomy (Bouvier, 1905b). Bouvier's monograph (1905a) contained an unfortunate number of errors, largely emanating from the Dendy-Fletcher controversy, some of which were pointed out in an otherwise complimentary postscript to Dendy's (1906) paper.

While Bouvier accepted Dendy's genus *Ooperipatus* '. . . by a series of unfortunate misprints, this name is in many places confounded with the name *Eoperipatus* given by Mr Evans to a totally distinct genus' (Dendy, 1906). Even more confusing was the designation of a species in a figure legend as *Ooperipatus leuckartii*. Bouvier retained these misconceptions in his second monograph (Bouvier, 1907). *Peripatoides orientalis* (designated *Peripatus leuckarti orientalis*, Fletcher, 1895) should have been *P. leuckartii; Ooperipatus*

TABLE 1

Chronological sequence of identification and synonomies of species of Australian peripatus

Author (date)	Designated Generic Names with			
Leuckart (1862)	*Peripatus* sp.			
Saenger (1869	*Peripatus Leuckartii*			
Dendy (1889a,b)			*Peripatus* sp.	
Dendy (1889c)			*Peripatus leuckartii*	
Dendy (1890b,c)				*Peripatus insignis* Victoria)
Pocock (1894)	*Peripatoides* designated as genus for Australasian species with *Peripatoides noveazealandiae* specified as type species			
Spencer (1895)				*Peripatus insignis* (Tasmania)
Dendy (1895a)				*Peripatus leuckartii*
Fletcher (1895)	*Peripatus leuckarti orientalis*		*Peripatus leuckarti* s.sp	*Peripatus leuckarti typica*
Dendy (1895b)			*Peripatus oviparus*	
Dendy (1900c)			*Ooperipatus oviparus*	*Ooperipatus insignis*
Bouvier (1907)	*Peripatoides orientalis*		*Ooperipatus oviparus*	*Ooperipatus leuckarti* / *Ooperipatus insignis*
Spencer (1909)				
Bouvier (1909a,b)				
Cockerell (1913)			*Symperipatus oviparus*	*Ooperipatus insignis* / *Ooperipatus spenceri*
Dakin (1914a,b)				
Bouvier (1915)				
Dakin (1920)				
Hardie (1972)	*Peripatoides leuckartii*		*Peripatoides oviparus*	*Peripatwides insignis*
Bachr (1977)				
Ruhberg (1985)	*Euperipatoides leuckarti*	Euperipatoides sp.	*Ooperipatus oviparus*	*Ooperipatellus insignis*
Ruhberg *et al.* (1988)				

Specific Sub-specific Epithets					
	Peripatus leuckarti occidentalis				
	Peripatoides occidentalis				
		Peripatoides gilesii			
		Peripatoides Woodwardi			
		Peripatoides gilesii			
			Ooperipatus paradoxus		
	Peripatoides occidentalis occidentalis	*Peripatoides occidentalis gilesii*			
	Peripatoides occidentalis	*Peripatoides gilesii*			
Ooperipatus decoratus			*Austroperipatus paradoxus*		
	Occiperipatoides occidentalis	*Occiperipatoides gilesi*	*Austroperipatus paradoxus*	*Mantonipatus persiculus*	
					Cephalofovea tomahmontis

leuckartii (designated *Peripatus leuckarti typica* by Fletcher, 1895) should have been *Ooperipatus insignis* (Dendy, 1890b,c). *Ooperipatus insignis* was designated by Bouvier only for the Tasmanian specimens previously considered identical to the Victorian *O. insignis* (Spencer, 1895) (see Table 1).

Despite the inappropriate species designations, Bouvier considered the Tasmanian oviparous form with fourteen pairs of legs to be specifically distinct from the oviparous species with the same number of legs from Victoria. It was soon realised that *O. insignis* from Tasmania as designated by Bouvier could not retain the name assigned to it, as *O. insignis* should have been retained by precedence for the Victorian species (Cockerell, 1908). Several years later the Tasmanian species was formally designated as *O. spenceri* after its discoverer (Cockerell, 1913), and it was suggested that the oviparous species with fifteen pairs of legs and the two oviparous species with fourteen pairs of legs should not be congeneric. Hence the genus *Symperipatus* was created to accommodate *O. oviparus*, and *Ooperipatus* was retained for *O. insignis* in Victoria and *O. spenceri* in Tasmania.

Following publication of his monographs, Bouvier examined two collections of peripatus made by Dr. E. Mjoberg during two expeditions in the period 1910-1913. In the first, from Western Australia, Bouvier could identify *P. woodwardi (= gilesii)* (Bouvier, 1915). In the second, from rainforest around Cairns in northern Queensland, he identified *O. oviparus*, extending the range of that species by more than 1,000km northwards. There were, in addition, a number of anomalous specimens in which females were viviparous, but possessed an apparent ovipositor, and where males evidenced a penis-like extension of the genital region. For simplicity Bouvier included this distinctive form within *Ooperipatus*, appending the specific name *paradoxus* (Bouvier, 1914; 1915).

Recent Studies

Following the works of Bouvier and Dakin on the Western Australian fauna, little was added to the taxonomy of Australian Onychophora for fifty years. In 1938 the first photograph ever taken of a peripatus was published, incorrectly identified as *O. insignis*. The specimen, from St. Marys in north-east Tasmania, clearly displays fifteen pairs of legs and is described in the accompanying note as being of a delicate fawn colour (Barrett, 1938). We believe that this specimen may be conspecific with the 'bleached' specimen in the Macleay Museum and have recently described it, from freshly collected individuals, as *Tasmanipatus barretti n.gen. n.sp.* together with a most unusual eyeless albino form, *T. anophthalmus n.sp.* (Ruhberg *et al.*, 1991).

In 1972 Mr Robert Hardie, of the University of New England, Armidale, submitted a thesis on various aspects of the distribution, ecology, behaviour and taxonomy of Australian onychophorans (Hardie, 1972). Some aspects of this work were later published (Hardie, 1975). This study provided, for the first time, an extensive analysis of the diagnostic characters that had been used by previous authors to distinguish species. In general, the anatomical characters employed for diagnosis were shown to be unsatisfactory for a variety of reasons. These included; characteristics found in all Australian species, characteristics that displayed intraspecific variation, characteristics that were sexually dimorphic, and characteristics that altered with the stage of development. Furthermore, some characters appeared to show clinal variation with altitude and latitude. Hardie concluded that the present state of taxonomy of Australian onychophorans was unsatisfactory and, until more extensive and rigorous work was carried out, a conservative approach should be adopted. All Australian onychophorans were accordingly grouped within the one genus *Peripatoides* to include the viviparous *leuckartii* in the east and *occidentalis* and *gilesii* in the west; and the oviparous *oviparus* in eastern mainland Australia and *insignis* in southern mainland Australia and Tasmania. Along with most

other workers, Hardie ignored Dakin's (1920) synonomy of *P. gilesii* and *P. occidentalis*. Hardie considered that *O. paradoxus* (later designated *Austroperipatus paradoxus* (Baehr, 1977)) should be disregarded until further information became available. A suggestion was made that macromolecular and cytogenetic techniques could be employed to unravel the problems of morphological taxonomy displayed by the group.

A world-wide revision of the family Peripatopsidae, including the Australian fauna, completely reversed these conclusions (Ruhberg, 1985). On the basis of morphological criteria, Ruhberg divided the Australian fauna into six genera containing eight species. *Austroperipatus paradoxus* was reinstated as a valid species, *Peripatoides leuckartii* was redescribed as *Euperipatoides leuckarti* (*Peripatoides* now being reserved for New Zealand species) and its distribution extended to the northwest of Tasmania. The Western Australian species *gilesii* and *occidentalis* were included in a single genus *Occiperipatoides*. The oviparous species *Ooperipatus oviparus* was reinstated (*Symperipatus oviparus* of Cockerell, 1913). *Ooperipatus insignis* from Victoria, *O. spenceri* and *O. decoratus* from Tasmania (the last designated for specimens collected at Dip River Falls near Wawbanna, northwest Tasmania, Baehr, 1977) and *O. viridimaculatus* from New Zealand were synonymized and given a new generic designation as *Ooperipatellus insignis*. Two new species, *Mantonipatus persiculus* from South Australia and *Euperipatoides* sp. from Armidale N.S.W., were also described. This version of the taxonomic relationships of Australian onychophorans is based entirely on morphological features with emphasis on the number of legs, the number and distribution of crural papillae and associated glands in the males, and reproductive mode in the females.

In 1984 we rediscovered the form of *P. leuckartii* in the Blue Mountains which displays crural papillae on only the first pair of legs (Fletcher, 1891) and, on allozyme and morphological criteria, have described it as *Cephalofovea tomahmontis* (Ruhberg *et al.*, 1988).

Conclusions

The confusion which has arisen in the taxonomy of Australian Onychophora is attributable to several factors. First, it has been extremely difficult to find clear-cut morphological features to distinguish species and genera in such a conservative group. Second, it has generally been assumed that species would have wide distributions, for example *O. oviparus* extending from Victoria to northern Queensland (Ruhberg, 1985). While some species are widely distributed over a diversity of habitat types (Van der Lande, 1978), our allozyme analysis indicates that many species have extremely limited ranges (Tait and Briscoe, 1990) and that collections made over wide geographical areas may include, as apparently intraspecific and clinal variation, variation which is truly interspecific (cf. Hardie, 1972). Third, this confusion is accentuated by sympatry of two or more species. *Ooperipatus oviparus* and *O. insignis* coexist at Macedon in Victoria (Dendy, 1890b,c; 1891a,b,c,d). Steel (1896; 1897) recorded both *P. leuckartii* and *O. oviparus* in the Moss Vale district of New South Wales, while Bouvier (1914; 1915) described *O. oviparus* and *O. paradoxus* from the Cairns region. In our own studies we have found up to three distinct species sympatric within the same rotten log (Briscoe and Tait, in preparation).

In addition to delineating and describing the species which make up the great radiation of onychophora in Australia we are also attempting to reconstruct the phylogenetic relationships among the forms. Our colleague Dr. D. Rowell, of the Australian National University, has very recently completed polynucleotide sequencing from some of the undescribed species. His results (Rowell, 1990, pers. comm.) support the hypothesis we derived from our allozyme data, that some of the separate lineages of onycho-

phorans in Australia are extremely ancient, having diverged at a date which may well precede the break-up of Gondwana.

ACKNOWLEDGEMENTS

We would like to thank Prof. David Spencer Smith and Dr. Peter Miller for providing facilities in the Zoology Department, University of Oxford, where the initial library research for this review was carried out. Margaret Clarke word-processed the manuscript. John Merrick, Ron Strahan and Jenny Harry provided constructive criticism of the manuscript. The photograph of *E. leuckartii* was provided by Ron Oldfield and the preparation of the scanning electron micrograph of the egg of *O. insignis* by Sue Doyle.

This work was partially supported by research grants from the Australian Research Council and Macquarie University. This is publication number 101 of the Research Unit for Biodiversity and Bioresources, Macquarie University.

References

ALEXANDER, A., 1957. — Notes on onychophoran behaviour. *Ann. Natal Mus.* 14: 35-43.

ANDERSON, D. T., 1966. — The comparative early embryology of the Oligochacta, Hirudinea and Onychophora. *Proc. Linn. Soc. N.S.W.* 91: 10-43.

——, and MANTON, S. M., 1972. — Studies on the Onychophora VIII. The relationship between the embryos and the oviduct in the viviparous onychophorans *Eoperipatus trinidadensis* Bouvier and *Macroperipatus torquatus* Kennel from Trinidad. *Phil. Trans. R. Soc. Lond.* B. 264: 161-189.

AX, P., 1984. — *Das Phylogenetische System.* Jena: Gustav Fischer Verlag.

BAEHR, VON M., 1977. — Über einige Onychophoren aus Australien und Tasmanien mit Beschreibung einer neuen Art und Anmerkungen zur Stellung von *Ooperipatus paradoxus* Bouvier 1915. *Zool. Jb. Syst.* 104: 9-19.

BARRETT, C., 1938. — A note on peripatus. *Vict. Nat.* 55: 11-12.

BELL, F. J., 1887. — Habitat of *Peripatus Leuckarti. Ann. Mag. Nat. Hist.* 20: 252.

BOUDREAUX, H. B., 1979. — Significance of intersegmental tendon system in arthropod phylogeny and a monophyletic classification of Arthropoda. *In*, GUPTA, A. P. (ed.) *Arthropod Phylogeny.* New York: Van Nostrand Reinhold.

BOUVIER, E. L., 1900. — Quelques observations sur les Onychophores (*Peripatus*) de la collection du Musée Britannique. *Q. J. microsc. Sci.* 43: 367-373.

——, 1902. — Moeurs des peripates. *Bull. Soc. entom. de France* 71: 110.

——, 1905a. — Monographie des Onychophores. *Annls. Sci. nat. (Zool.)* 2: 1-383. Pl. 1-13.

——, 1905b. — Sur l'organisation du *Peripatoides orientalis* Fletcher, *P. Leuckarti* de la plupart des auteurs. *C.R. Soc. de Biol. Paris* 54: 1033-1034.

——, 1907. — Monographie des Onychophores. *Annls. Sci. nat. (Zool.)* 5: 61-318.

——, 1909a. — Sur un nouvel Onychophore australien. *C.R. Acad. Sci. nat. Paris* 148: 1292-1294.

——, 1909b. — Onychophora. *In*, Die Fauna Sudwest Australians. Ergebnisse der Hamburger sudwestaustralischen Forschungsreise 1905 herausgegeben van Prof. Dr. W. Michaelsen und Dr. R. Hartmeyer. Jena: Verlag von Gustav Fischer. 2(18): 315-328.

——, 1914. — Nouvelle observations sur la viviparite chez les Onychophores australiens. *C.R. Acad. Sci. Paris* 158: 1547-1550.

——, 1915. — Onychophora. In Results of Dr. E. Mjoberg's Swedish scientific expeditions to Australia 1910-1913. *Ark. Zool.* 10: 1-23.

BRINCK, P., 1956. — Onychophora. A review of the South African species, with a discussion on the significance of the geographical distribution of the group. *In*, HANSTROM, B., BRINCK, P. and RUDEBECK, G. (eds.) *South African Animal Life. Volume 4.* Uppsala: Almquist and Wiksell.

CLARKE, K. U., 1979. — Visceral anatomy and arthropod phylogeny. *In*, GUPTA, A. P. (ed.) *Arthropod Phylogeny.* New York: Van Nostrand Reinhold.

COCKERELL, T. D. A., 1908. — A review of Monographie des Onychophores by E. L. Bouvier. *Science* 27: 619-621.

——, 1913. — A note on the Australian Peripatopsidae. *In* CLARK, A. H. A revision of the American species of *Peripatus. Proc. Biol. Soc. Washington* 26: 1-19.

CUENOT, L., 1949. — Les Onychophores. *In* GRASSE, P. P. (ed.) *Traite de Zoologie.* Volume 6. Paris: Masson et Cie.

DAKIN, W. J., 1914a. — Fauna of Western Australia 1. The Onychophora of Western Australia. *Proc. Zool. Soc. Lond.* 289-292.
——, 1914b. — The Onychophora of Western Australia. *J. West. Aust. Nat. Hist. Soc.* 5: 3-5.
——, 1920. — Fauna of Western Australia III. Further contributions to the study of the Onychophora. The anatomy and systematic position of West Australian *Peripatoides*, with an account of certain histological details of general importance in the study of *Peripatus*. *Proc. Zool. Soc. Lond.* 367-389. Pl. 1-5.
DENDY, A., 1889a. — *Peripatus* in Victoria. *Vict. Nat.* 5: 134-135.
——, 1889b. — *Peripatus* in Victoria. *Nature* 39: 366.
——, 1889c. — Observations on the Australian species of *Peripatus*. *Proc. Roy. Soc. Vict.* 2: 50-62.
——, 1890a. — Zoology: Invertebrata. *In* SPENCER, W., BALDWIN (ed.) *Handbook of Victoria. Australasian Association for the Advancement of Science*. Melbourne: Spectator Publ.
——, 1890b. — Preliminary account of a new Australian *Peripatus*. *Vict. Nat.* 6: 173-176.
——, 1890c. — Preliminary account of a new Australian *Peripatus*. *Ann. Mag. Nat. Hist.* 6: 121-123.
——, 1891a. — An oviparous species of *Peripatus*. *Nature* 44: 468.
——, 1891b. — The reproduction of *Peripatus leuckartii*, Saenger. *Zool. Anz.* 14: 461-463.
——, 1891c. — Note on the mode of reproduction of *Peripatus leuckartii*. *Vict. Nat.* 8: 67.
——, 1891d. — On the oviparity of *Peripatus leuckartii*. *Proc. Roy. Soc. Vict.* 4: 31-34.
——, 1892a. — Further observations on the eggs of *Peripatus*. *Report of the 4th Meeting of the Australasian Association for the Advancement of Science. Hobart, Tasmania*, Section D: 375-380.
——, 1892b. — Further notes on the oviparity of the larger Victorian *Peripatus*, generally known as *P. leuckartii*. *Proc. Linn. Soc. N.S.W.* 7: 267-276.
——, 1892c. — Further notes on the oviparity of the larger Victorian *Peripatus*, generally known as *P. leuckartii*. *Proc. Roy. Soc. Vict.* 5: 27-35.
——, 1893a. — The hatching of a peripatus egg. *Nature* 47: 508-509.
——, 1893b. — The hatching of a peripatus egg. *Proc. Roy. Soc. Vict.* 6: 118-119.
——, 1894a. — Note on a new variety of *Peripatus novae-zealandiae*, Hutton. *Trans. Proc. N.Z. Instit.* 27: 190-191.
——, 1894b. — Additions to the cryptozoic fauna of New Zealand. *Ann. Mag. Nat. Hist.* 14: 393-401.
——, 1895a. — The cryptozoic fauna of Australasia. *Report of the 6th meeting of the Australasian Association for the Advancement of Science. Brisbane, Queensland.* Presidential Address, Section D: 99-119.
——, 1895b. — Description of *Peripatus oviparus*. *Proc. Linn. Soc. N.S.W.* 10: 195-200.
——, 1895c. — Preliminary Notes on the reproductive organs of *Peripatus oviparus*. *Zool. Anz.* 18: 264-266.
——, 1900a. — A new peripatus from New Zealand. *Nature* 61: 444.
——, 1900b. — Note on and exhibition of a new species of *Peripatus (P. viridimaculatus)* from New Zealand. *Trans. Proc. N.Z. Instit.* 32: 436.
——, 1900c. — Preliminary note on a proposed new genus of Onychophora. *Zool. Anz.* 23: 509-511.
——, 1902. — On the oviparous species of Onychophora. *Q. J. microsc. Sci.* 45: 363-415. Pl. 19-22.
——, 1906. — Note on the supposed type specimen of *Peripatus leuckarti* Saenger and on the nomenclature of the Australian Onychophora. *Zool. Anz.* 30: 175-177.
DODDS, S. E., and EWER, D. W., 1952. — On the rate of water loss in *Peripatopsis moseleyi*. *Ann. Natal Mus.* 12: 275-278.
DZIK, J., and KRUMBIEGEL, G., 1989. — The oldest 'onychophoran' *Xenusion*: a link connecting phyla? *Lethaia* 22: 169-181.
EVANS, R., 1901a. — On two new species of Onychophora from the Siamese Malay States. *Q. J. microsc. Sci.* 44: 473-538. Pl. 32-37.
——, 1901b. — On the Malayan species of Onychophora. Part II. The development of *Eoperipatus weldoni*. *Q. J. microsc. Sci.* 45: 41-88. Pl. 5-9.
FIELD, K. G., OLSEN, G. J., LANE, D. J., GIOVANNONI, S. J., GHISELIN, M. T., RAFF, E. C., PACE, N. R., and RAFF, R. A., 1988. — Molecular phylogeny of the animal kingdom. *Science* 239: 748-753.
FLETCHER, J. J., 1887. — Note and exhibition of a specimen of *Peripatus* from Warragul, Victoria. *Proc. Linn. Soc. N.S.W.* 2: 450.
——, 1888a. — Note and exhibition of specimens of *Peripatus* from Wollongong N.S.W. *Proc. Linn. Soc. N.S.W.* 3: 892-894.
——, 1888b. — Note and exhibition of new-born *Peripatus*. *Proc. Linn. Soc. N.S.W.* 3: 1508.
——, 1888c. — Note and exhibition of two specimens of *Peripatus* from Burrawang N.S.W. *Proc. Linn. Soc. N.S.W.* 3: 1560.
——, 1890. — Additional notes on *Peripatus leuckarti*. *Proc Linn. Soc. N.S.W.* 5: 469-486.
——, 1891a. — Note in reply to Dr. Dendy's recent article on oviparity in *Peripatus leuckartii*. *Proc. Linn. Soc. N.S.W.* 6: 577.
——, 1891b. — Note and exhibition of a specimen of *P. leuckarti* from the Blue Mountains. *Proc. Linn. Soc. N.S.W.* 6: 167.
——, 1892a. — Note and exhibition of newly born young of *Peripatus*. *Proc. Linn. Soc. N.S.W.* 7: 40.
——, 1892b. — A viviparous Australian peripatus (*P. leuckartii* Saeng.). *Proc. Linn. Soc. N.S.W.* 7: 179-196.

——, 1895. — On the specific identity of the Australian *Peripatus* usually supposed to be *P. leuckarti*, Saenger. *Proc. Linn. Soc.* N.S.W., 10: 172-194.

——, 1900. — Note and exhibition of a peripatus from New Zealand. *Proc. Linn. Soc.* N.S.W. 25: 116.

FLYNN, T. T., 1918. — The distribution of *Anaspides* and *Ooperipatus* in Tasmania. *Aust. Zool.* 1: 102.

GERVAIS, M., 1837. — Études pour servir a l'histoire naturelle des Myriapodes. *Ann. Sc. nat.* 7: 35-60.

GHISELIN, M. T., 1984. — Peripatus as a Living Fossil. *In* ELDREDGE, N., and STANLEY, S. M. (eds.) *Living Fossils*. New York: Springer Verlag.

——, 1985. — A movable feaster. *Nat. Hist.* 9: 54-61.

GRUBE, E., 1853. — Untersuchungen über den Bau von *Peripatus Edwardsii*. *Muller's Arch. f. Anat. u. Phys.*: 322-360. Pl. 9 , 10.

GUILDING, L., 1826. — Mollusca Caribbocana. No. 2. An account of a new genus of Mollusca. *Zool. J.* 2: 443-444. Pl. 14.

HADDON, K., 1913. — Notes on *Peripatoides woodwardi* Bouvier. *Proc. Zool. Soc. Lond.* 81: 611-613.

HARDIE, R., 1972. — Studies on the Onychophora. Armidale, N.S.W.: University of New England, M.Sc. thesis, unpubl.

——, 1975. — The riddle of *Peripatus*. *Aust. Nat. Hist.* 18: 180-185.

HELMS, R , 1890. — Report of a collecting trip to Mt. Kosciusko. *Rec. Aust. Mus.* 1: 11-16.

HEYLER, D., and POPLIN, C. M., 1988. — The fossils of Montceau-les-Mines. *Scientif. Amer.* 259: 70-76.

HILL, R. P., 1950. — *Peripatus*: a missing link. *Discovery, London* 11: 14-18.

HOLLIDAY, R. A., 1942. — Some observations on Natal Onychophora. *Ann. Natal Mus.* 10: 237-244. Pl. 5-10.

JAEGER, H., and MARTINSSON, A., 1967. — Remarks on the problematic fossil *Xenusion anerswaldae*. *Geol. For. Stockh. Forh.* 88: 435-452.

JAMIESON, B. G. M., 1986. — Onychophoran — euclitellate relationships: evidence from spermatozoal ultrastructure. *Zoologica Scripta* 15: 141-155.

——, 1987. — *The Ultrastructure and Phylogeny of Insect Spermatozoa*. Cambridge: Cambridge University Press.

KRUMBIEGEL, G., DEICHFUSS, H., and DEICHFUSS, H., 1980. — Ein neuer fund von *Xenusion*. *Hallesches Jh. für Geowissenschaf.* 5: 97-99.

LAVALLARD, R., and CAMPIGLIA, S., 1975. — Contribution to the biology of *Peripatus acacioi* Marcus and Marcus (Onychophore) 5. Studies of the breeding in a laboratory culture. *Zool. Anz.* 195: 338-350.

LEUCKART, R., 1862. — Bericht uber die wissenschaftlichen Leistungen in der Naturgeschichte der niederen Thiere wahrend des Jahres 1860. *Archio. für Naturgesch.* 27: 235.

——, 1869. — Bericht uber die wissenschaftlichen Leistungen in der Naturgeschichte der niederen Thiere wahrend der Jahres 1868 und 1869. *Archiv. für Naturgesch.* 35: 277.

——, 1871. — Bericht uber die wissenschaftlichen Leistungen in der Naturgeschichte der niederen Thiere wahrend der Jahres 1870 und 1871. *Archiv. für Naturgesch.* 37: 406-407.

MACLEAY, W. S., 1829. — Notes on the genus *Capromys* of Desmarest. *Zool. J.* 4: 278.

MANGUM, C. P., SCOTT, J. L., BLACK, R. E. L., MILLER, K. I., and VAN HOLDE, K. E., 1985. — Centipedal hemocyanin: its structure and its implications for arthropod phylogeny. *Proc. Natl. Acad. Sci.* 82: 3721-3725.

MANTON, S. M., 1938a. — Studies on the Onychophora VI. The life history of *Peripatopsis*. *Ann. Mag. Nat. Hist.* 1: 515-529.

——, 1938b. — Studies on the Onychophora IV. The passage of spermatozoa into the ovary in *Peripatopsis* and the early development of the ova. *Phil. Trans. R. Soc. Lond.* B. 228: 421-441. Pl. 50-51.

——, 1949. — Studies on the Onychophora VII. The early embryonic stages of *Peripatopsis* and some general considerations concerning the morphology and phylogeny of the Arthropoda. *Phil. Trans. R. Soc. Lond.* B. 233: 483-580.

——, and ANDERSON, D. T., 1979. — Polyphyly and the evolution of arthropods. *In* HOUSE, M. R. (ed). *The Origin of Major Invertebrate Groups*. London: Academic Press.

——, and HEATLEY, N. G., 1937. — Studies on the Onychophora II. The feeding, digestion, excretion and food storage of *Peripatopsis*. *Phil. Trans. R. Soc. Lond.* B. 227: 411-464. Pl. 38-40.

——, and RAMSAY, A., 1937. — Studies on the Onychophora III. On the control of water loss in *Peripatopsis*. *J. exp. Biol.* 14: 470-472.

MORRISON, P. R., 1946. — Physiological observations on water loss and oxygen consumption in *Peripatus*. *Biol. Bull.* 91: 181-188.

MOSELEY, H. N., 1874. — On the structure and development of *Peripatus capensis*. *Phil. Trans. R. Soc. Lond.* B. 164: 757-782.

NEWLANDS, G. and RUHBERG, H., 1978. — Onychophora. *In* WERGER, M. J. A. (ed) *Bigeography and Ecology of South Africa*. The Hague: W. Junk.

OLLIFF, A. S., 1887. — Note and exhibition of a specimen of *Peripatus* from Cassilis, N.S.W. *Proc. Linn. Soc. N.S.W.* 2: 981.

PAULDEN, F., 1898. — *Peripatus leuckarti*. *Trans. Ann. Rep. Manch. micro. Soc.* 37-44. Pl. 6, 7.

POCOCK, R. I., 1894. — Contributions to our knowledge of the arthropod fauna of the West Indies Part 3. Diplopoda and Malacopoda with a supplement on the Arachnida of the class Pedipalpi. *J. Linn. Soc. (Zool.) Lond.* 24: 473-544.

POMPECKJ, J. F., 1927. — Ein neues Zeugnis uralten Lebens. *Palaeontol. Z.* 9: 287-313.

READ, V. M. ST. J., and HUGHES, R. N., 1987. — Feeding behaviour and prey choice in *Macroperipatus torquatus* (Onychophora). *Proc. R. Soc. Lond.* B. 230: 483-506.

ROBISON, R. A., 1985. — Affinities of *Aysheaia* (Onychophora), with description of a new Cambrian species. *J. Paleo.* 59: 226-235.

RUHBERG, H., 1985. — Die Peripatopsidae (Onychophora). Systematik, Okologie, Chorologie und Phylogenetische Aspekte. *Zoologica* 137: 1-183.

——, MESIBOV, R., BRISCOE, D. A., and TAIT, N. N., 1991. — *Tasmanipatus barretti* n. gen., n.sp. and *T. anophthalmus* n.sp.; preliminary note on two new and unusual Peripatopsidae (Onychophora) from north-east Tasmania. *Pap. Proc. R. Soc. Tasm.* (in press).

——, TAIT, N. N., BRISCOE, D. A., and STORCH, V., 1988. — *Cephalofovea tomahmontis* n. gen., n.sp., an Australian peripatopsid (Onychophora) with a unique cephalic pit. *Zool. Anz.* 221: 117-133.

SAENGER, H., 1869. — *Peripatus capensis* Sr and *Peripatus Leuckartii* n.sp. *Transactions of the Second Congress of Russian Naturalists in Moscow.* pp.239-262; translated into French: BOUVIER, E. L., 1901. A propos d'un travail de H. Sänger sur les Peripates. *Bull. Soc. Phil. (Paris)* 3: 9-36, Pl. 12-13.

SCHALLER, F., 1979. — Significance of sperm transfer and formation of spermatophores in arthropod phylogeny. *In* GUPTA, A. P. (ed.) *Arthropod Phylogeny.* New York: Van Nostrand Reinhold.

SEDGWICK, A., 1885. — The development of *Peripatus capensis* Part I. *Q. J. microsc. Sci.* 25: 449-468. Pls 31, 32.

——, 1888. — A monograph on the species and distribution of the genus *Peripatus* (Guilding). *Q. J. micros. Sci.* 28: 431-493. Pl. 34-40.

——, 1889. — *Peripatus* in Australia. *Nature* 39: 412-413.

——, 1891. — An oviparous species of *Peripatus. Nature* 44: 494.

——, 1908. — The distribution and classification of the Onychophora. *Q. J. microsc. Sci.* 52: 379-406.

SHELDON, L., 1888. — On the development of *Peripatus novae-zealandiae. Q. J. microsc. Sci.*, 28: 205-237.

SKUSE, F. A. A., 1897. — Additional localities for *Peripatus leuckartii-Säng. Rec. Aust. Mus.* 3: 10-11.

SPENCER, W. B., 1892. — A trip to Queensland in search of *Ceratodus. Vict. Nat.* 9: 16-32.

——, 1895. — Note on the presence of *Peripatus insignis* in Tasmania. *Proc. Roy. Soc. Vict.* 7: 31-32.

——, 1909. — Description of a new species of *Peripatoides* from West Australia. *Proc. Roy. Soc. Vict.* 21: 420-422.

STEEL, T., 1896. — Observations on peripatus. *Proc. Linn. Soc. N.S.W.* 21: 94-103.

——, 1897. — Note on *Peripatus. Proc. Linn. Soc. N.S.W.* 22: 124-125.

——, 1925. — *Peripatus. In* JOSE, A. W. and CARTER, H. J. (eds.) *Australian Encyclopaedia.* Sydney: Angus and Robertson.

STORCH, V., and RUHBERG, H., 1977. — Zur Entstehung der Spermatophore von *Opisthopatus cinctipes* Purcell, 1899 (Onychophora, Peripatopsidae). *Zoomorphologie* 87: 263-276.

TAIT, N. N., and BRISCOE, D. A., 1989. — Peripatus. *Aust. Nat. Hist.* 22: 573-578.

——, and ——, 1990. — Sexual head structures in the Onychophora: unique modifications for sperm transfer. *J. Nat. Hist.* (in press).

THOMPSON, I., and JONES, D. S., 1980. — A possible onychophoran from the Middle Pennsylvanian Mazon Creek beds of northern Illinois. *J. Paleo.* 54: 588-596.

TRYON, H., 1887. — On *Peripatus* and its occurrence in Australia. *Proc. Roy. Soc. Qd.* 4: 78-85.

VAN DER LANDE, V., 1978. — The occurrence, culture and reproduction of *Peripatoides gilesii* Spencer (Onychophora) on the Swan Coastal Plain. *West. Aust. Nat.* 14: 29-35.

WAITE, E. R., 1895. — Note and exhibition of peripatus from Colo Vale N.S.W. and a record from Moree N.S.W. *Proc. Linn. Soc. N.S.W.* 10: 549.

WALCOTT, C. D., 1911. — Cambrian geology and palaeontology no. 5, Middle Cambrian annelids. *Smithsonian misc. Collect.* 57: 110-144.

WILLEY, A., 1898. — Anatomy and development of *Peripatus novae-brittaniae. Zoological Results, Cambridge* 1: 1-52.

WHITTINGTON, H. B., 1978. — The lobopod animal *Aysheaia pedunculata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Phil. Trans. R. Soc. Lond.* B. 284: 165-197.

WOODWARD, B. H., 1906. — Further notes on *Peripatus. J. West Aust. Nat. Hist. Soc.* 3: 10.

WRIGHT, J. C., and LUKE, B. M., 1989. — Ultrastructural and histochemical investigations of *Peripatus* integument. *Tissue and Cell* 21: 605-625.